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PHENOLOGY OF THE VEGETATION IN THE HESTER MALAN NATURE RESERVE IN THE NAMAQUALAND BROKEN VELD:

2. THE THEROPHYTE POPULATION

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Abstract

The quantitative seasonal changes in therophyte populations were investigated by making monthly counts of the total number of plants in five, 1 m^2 plots. Densities ranged between 115 and 1 810 seedlings per m^2 in April. Of the total of 5 056 seedlings that emerged on the plots, 63,59 % reached maturity. The survival pattern varied between species as well as plots, but no clear relationships between the mortality of a plant species and particular abiotic factors could be demonstrated.

Uittreksel

'N FENOLOGIESE STUDIE VAN DIE PLANTEGROEI VAN DIE NAMAKWALANDSE GEBROKE VELD:
2. DIE TEROFITIESE BEVOLKING

Die kwantitatiewe seisoenale veranderings in terofitiese plantbevolkings is aan die hand van vyf, 1 m^2 persele ondersoek, waarop die aantal plante maandeliks aangeteken is. Digthede van 115 tot 1 810 saailinge per m^2 is in April aangeteken. Van die totale 5 056 saailinge wat op die persele voorgekom het, het 63,59 % volwassenheid bereik. Verskillende spesies het verskillende oorlewingspatrone getoon, terwyl die persentasie oorlewing ook van perseel tot perseel gewissel het. Geen duidelike verband tussen die afsterwing van individue van 'n plantspesie en bepaalde abiotiese faktore kon aangetoon word nie.

Introduction

Although the perennial species undergo definite seasonal changes in appearance, it is the pronounced fluctuations in the ephemeral population of the region with its display of spring flowers which mainly attract attention. Not only do the ephemeral populations vary considerably between seasons and localities within a single year, but also from one year to another. For the seeds of the therophyte species to germinate and the seedlings to develop into mature plants in large numbers, a succession of specific environmental conditions is necessary. Due to the erratic nature of some of these conditions the seeds often fail to germinate. In some years many seedlings are produced, yet most perish before maturity. Consequently only once in about ten years, on average, do dense stands of therophytes develop in Namaqualand.

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Although many workers (Talbot, Biswell and Hormay, 1939; Went, 1948, 1949, 1955; Went and Westergaard, 1949; Juhren, Went and Phillips, 1956; Tevis, 1958a, 1958b; Beatley, 1967; Bykov, 1974) recognized seasonal fluctuations in the density and composition of desert therophyte populations, these fluctuations are not yet fully understood. From studies in the south eastern Californian portion of the Mojave Desert, Went (1955) concluded that desert annuals, once germinated, usually reach maturity, if only as depauperate and barely reproductive plants. The figures provided by Tevis (1958b) for the Sonoran Desert in California and Beatley (1967) for the northern Mojave Desert in Nevada, however, indicate that it rarely happens that more than 50 % of the seedlings survive. Similar studies had not been undertaken in Namaqualand prior to the present investigation which attempts to measure changes in the composition of therophyte populations during a growing season. The results presented in this paper are from a restricted area and for one season only and are therefore not offered as norms for describing the whole Namaqualand Broken Veld.

METHODS

After the good rains (55,5 mm) which fell in March 1974, five areas with fairly dense stands of therophyte seedlings were selected in April 1974 in the Hester Malan Nature Reserve near Springbok (Rösch, 1977; Van Rooyen, Theron and Grobbelaar, 1979). In each of five areas a square metal frame was permanently placed so as to include a representative portion of that area. The position of every seedling within the plots was carefully mapped on graph paper. The plots were visited at monthly intervals until September 1974. During these visits the positions of new seedlings were mapped while the death of others was noted. During the last visit (in September), those therophyte individuals which, though still alive, were on the verge of dying and had not yet flowered, were excluded from the September count. Only in the case of seedlings of perennial species, were immature plants included in the September count. Although the seedlings of perennial species are not part of the therophyte population, they were included in the monthly counts because it was impossible to identify all species during the first few months. Barring plot 5, where a substantial number of these seedlings occurred, only six other seedlings of perennial species were noted, three in each of plots 1 and 2.

RESULTS AND DISCUSSION

The experimental plots

Some of the physical characteristics of the plots are summarized in Table 1. Although a few therophyte species occurred in several plots, no two plots had the same species composition (Table 2).

TABLE 1

Selected characteristics of the phenological study sites in the Hester Malan Nature Reserve

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Height above sea level (m)	1 180	1 210	1 260	1 260	1 080
Slope	—	5°	—	5°	—
Aspect	—	WNW	—	SSW	—
Geological formation	Transition	Gneiss	Transition	Granitic gneiss	Gneiss
Surface erosion (1–4)*	3	3	2	2	4
Stoniness (0–5)*	2	3	0	2	0
Soil depth (m)	0,3	0,25	>0,5	0,3	0,35
Biotic influences	Insect damage	Insect damage Grazing	Insect damage Grazing	Insect damage	Insect damage Grazing
Disturbance	Alongside road	—	Abandoned land	Old "kraal"	Water course

*Scale according to Loxton (1966)

TABLE 2

Species composition of the five plots used for phenological studies in the Hester Malan Nature Reserve. Perennial plant species are included and marked with an asterisk

Species	Plot				
	1	*2*	*3*	*4*	*5*
Aizoon canariense	×	×		×	×
*Aptosimum indivisum					×
Arctotis fastuosa	×			×	×
Cotula barbata			×		
Crotalaria micrantha	×		×		
Diascia tanyceras	×				
Dimorphotheca sinuata	×	×			×
Dischisma spicatum	×		×		
Erodium cicutarium	×			×	
Felicia merxmuelleri	×			×	
*Galenia africana	×				×
G. filiformis	×	×		×	
Helichrysum obtusum var. obtusum	×		×		
Heliophila pectinata	×	×		×	
H. variabilis			×		
*Hermannia meyeriana			×		
*Herrea blanda			×		
*Hypertelis salsoloides					×
Ifloga paronychioides	×				
Karroochloa schismoides		×			
*Lachenalia ovatifolia			×		
*Lebeckia sericea		×			
*Leyssera gnaphalioides			×		
L. tenella	×	×		×	
Lotononis depressa					×
Manulea cheiranthus	×	×			
Mesembryanthemum karrooense			×	×	
Mesembryanthemum sp.			×		
Micropterum papulosum	×	×			
Nemesia azurea		×			×
Osteospermum amplectens		×			×
O. hyoseroides	×	×			×
*Oxalis campylorrhiza					×
*O. furcillata					×
*O. obtusa	×	×	×	×	×
*Peliostomum virgatum					×
*Pentaschistis tomentella			×		
Pentzia albida				×	
P. suffruticosa				×	
Pharnaceum croceum			×		
Polycarena pubescens			×		
Schismus barbatus	×	×		×	
Senecio cardaminefolius	×			×	
Tetragonia microptera	×	×		×	
*Trachyandra flexifolia	×		×		
*Trachyandra sp.				×	
Ursinia cakilefolia			×		
U. calenduliflora					×
U. nana subsp. nana	×			×	×
Zaluzianskya benthamiana	×			×	×

Plot 1

In plot 1 *Micropterum papulosum*, a small inconspicuous prostrate therophyte, was the most abundant species (Table 3). The seedlings of *Leyssera tenella, Dischisma spicatum, Erodium circutarium, Zaluzianskya benthamiana* and *Ursinia nana* subsp. *nana* did not develop into large plants but nevertheless produced a few flowers. *Tetragonia microptera, Aizoon canariense, Galenia filiformis* and *Ifloga paronychioides* were less numerous but are also relatively inconspicuous species. Although not very abundant, *Osteospermum hyoseroides* was the most conspicuous species in plot 1.

Plot 2

This plot (Table 4), like plot 5, contained considerably less seedlings than the other sites (Tables 3 to 7). Although *Tetragonia microptera* plants were more abundant than *Osteospermum hyoseroides* plants, the latter appeared to be the dominant species because they were larger and more conspicuous. A significant feature of this plot was the large number of *Heliophila pectinata* seedlings which emerged in July.

Plot 3

Cotula barbata dominated this site (Table 5) both in numbers and appearance. These plants, however, were very small and consisted of a few leaves at the base and a solitary inflorescence. In many cases the leaves could no longer be distinguished by the time the inflorescence was produced. Despite high mortality rates, *Dischisma spicatum* and *Pharnaceum croceum* were fairly conspicuous during September. The following perennial species, which sprouted after their dormant period during summer, were noted in the plot in April: *Pentaschistis tomentella, Leyssera gnaphalioides, Lachenalia ovatifolia, Trachyandra flexifolia* and *Oxalis obtusa.*

Plot 4

In this plot *Leyssera tenella* was the most abundant species (Table 6). These plants remained small and produced few flowers. The *Arctotis fastuosa* plants also did not grow much and started flowering at an early date. In this plot there were several species such as *Pentzia albida* and *P. suffruticosa* whose seeds germinated over a long period—from March to June.

Plot 5

This plot (Table 7) displayed the smallest number of plants throughout the experimental period. Seedlings of perennial species, such as *Peliostomum virgatum* and *Hypertelis salsoloides* occurred in fairly large numbers in this plot. Another noteworthy aspect of plot 5 was the large number of *Oxalis* plants which emerged from it.

TABLE 3

The size and composition of the population of plot I (1 m^2) in the Hester Malan Nature Reserve as determined at monthly intervals from April to September 1974

	April			May			June			July			August			September		
Species	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Micropterum papulosum	859	73,04	100,00	777	70,83	90,45	660	71,82	76,83	565	69,58	65,77	483	68,03	56,23	449	67,82	52,27
Leyssera tenella	135	11,48	100,00	133	12,12	98,52	112	12,19	82,96	108	13,30	80,00	99	13,94	73,33	92	13,90	68,15
Tetragonia microptera	55	4,68	100,00	53	4,83	96,36	36	3,92	65,45	19	2,34	34,55	13	1,84	23,64	12	1,81	21,82
Dischisma spicatum	26	2,21	100,00	26	2,37	100,00	14	1,52	53,85	11	1,35	42,31	9	1,27	34,62	9	1,36	34,62
Erodium cicutarium	19	1,62	82,61	23	2,10	100,00	20	2,18	86,96	21	2,59	91,30	21	2,96	91,30	20	3,02	86,96
Zaluzianskya benthamiana	18	1,53	90,00	20	1,82	100.00	18	1,96	90,00	12	1,48	60,00	11	1,55	55,00	11	1,66	55,00
Ursinia nana subsp. nana	12	1,02	100,00	11	1,00	91,67	10	1,09	83,33	11	1,35	91,67	9	1,27	75,00	8	1,21	66,67
Osteospermum hyoseroides	10	0,85	100,00	10	0,91	100,00	10	1,09	100,00	10	1,23	100,00	10	1,41	100,00	10	1,51	100,00
Aizoon canariense	8	0,68	100,00	8	0,73	100,00	7	0,76	87,50	7	0,86	87,50	7	0,99	87,50	6	0,91	75,00
Galenia filiformis	6	0,51	100,00	6	0,57	100,00	5	0,54	83,33	5	0,62	83,33	5	0,70	83,33	5	0,76	83,33
Ifloga paronychioides	6	0,51	85,71	7	0,64	100,00	5	0,54	71,43	6	0,74	85,71	6	0,84	85,71	6	0,91	85,71
Dimorphotheca sinuata	5	0,43	100,00	5	0,46	100,00	4	0,44	80,00	4	0,49	80,00	4	0,56	80,00	4	0,60	80,00
Helichrysum obtusum var. obtusum	5	0,43	100,00	5	0,46	100,00	5	0,54	100,00	5	0,62	100,00	4	0,56	80,00	4	0,60	80,00
Manulea cheiranthus	4	0,34	100,00	4	0,36	100,00	4	0,44	100,00	2	0,25	50,00	2	0,28	50,00	2	0,30	50,00
Arctotis fastuosa	3	0,26	100,00	3	0,27	100,00	3	0,33	100,00	2	0,25	66,67	2	0,28	66,67	2	0,30	66,67
Crotalaria micrantha	3	0,26	100,00	2	0,18	66,67	1	0,11	33,33	0	0,00	0,00	0	0,00	0,00	0	0,00	00,00
Diascia tanyceras	1	0,09	100,00	1	0,09	100,00	1	0,11	100,00	1	0,12	100,00	1	0,14	100,00	1	0,15	100.00
*Galenia africana	1	0,09	100,00	1	0,09	100,00	1	0,11	100,00	1	0,12	100,00	1	0,14	100,00	1	0,15	100,00
*Species 1				2	0,18	100,00	2	0,22	100,00	2	0,25	100,00	2	0,28	100,00	2	0,30	100,00
Schismus barbatus							1	0,11	12,50	6	0,74	75,00	8	1,13	100,00	8	1,21	100,00
Senecio cardaminefolius										10	1,23	100,00	8	1,13	80,00	6	0,91	60,00
Heliophila pectinata										3	0,37	100,00	3	0,42	100,00	3	0,45	100,00
Felicia merxmuelleri										1	0,12	50,00	2	0,28	100,00	1	0,15	50,00
Total	1 176	100,03		1 097	100,01		919	100,02		812	100,00		710	99,99		662	99,99	
d			100,00			90,59			75,89			67,05			58,63			54,67

* Perennial species.

a. Number of live individuals present.

b. Number of live individuals present as a percentage of the month's total live plant population = relative abundance.

c. Number of live individuals present as a percentage of the largest monthly live count for this species during the whole experimental period (6 months)—PMP (Percentage of Maximum Presence).

d. Total number of live individuals on plot as a percentage of the total number of seedlings that emerged during the whole experimental period (6 months).

TABLE 4

The size and composition of the population of plot 2 (1 m²) in the Hester Malan Nature Reserve as determined at monthly intervals from April to September 1974

	April			May			June			July			August			September		
Species	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Tetragonia microptera	137	68,84	100,00	129	68,98	94,16	98	63,64	71,53	78	44,83	56,93	69	43,95	50,36	61	41,78	44,53
Osteospermum hyoseroides	38	19,10	100,00	35	18,72	92,11	35	22,73	92,11	33	18,97	86,84	33	21,02	86,84	31	21,23	81,58
Galenia filiformis	7	3,52	100,00	7	3,74	100,00	5	3,25	71,43	5	2,87	71,43	5	3,18	71,43	5	3,43	71,43
Dimorphotheca sinuata	6	3,02	100,00	6	3,21	100,00	6	3,90	100,00	5	2,87	83,33	5	3,18	83,33	5	3,43	83,33
Aizoon canariense	5	2,51	100,00	5	2,67	100,00	4	2,60	80,00	2	1,15	40,00	1	0,64	20,00	0	0,00	0,00
Osteospermum amplectens	3	1,51	100,00	2	1,07	66,67	2	1,30	66,67	2	1,15	66,67	2	1,27	66,67	2	1,37	66,67
*Lebeckia sericea	1	0,50	100,00	1	0,53	100,00	1	0,65	100,00	1	0,57	100,00	1	0,64	100,00	1	0,68	100,00
Manulea cheiranthus	1	0,50	50,00	1	0,53	50,00	1	0,65	50,00	2	1,15	100,00	2	1,27	100,00	2	1,37	100,00
Micropterum papulosum	1	0,50	100,00	1	0,53	100,00	1	0,65	100,00	1	0,57	100,00	1	0,64	100,00	1	0,68	100,00
Heliophila pectinata							1	0,65	3,57	28	16,09	100,00	28	17,83	100,00	26	17,81	92,86
Schismus barbatus										3	1,72	50,00	4	2,55	66,67	6	4,11	100,00
Karroochloa schismoides										1	0,57	100,00	1	0,64	100,00	1	0,68	100,00
Leyssera tenella										1	0,57	33,33	3	1,91	100,00	2	1,37	66,67
Nemesia azurea										1	0,57	100,00	1	O,64	100,00	1	0,68	100,00
*Species 2										1	0,57	100,00	1	0,64	100,00	1	0,68	100,00
*Species 3																1	0,68	100,00
Total	199	100,00		187	99,98		154	100,02		164	100,00		157	100,00		146	99,96	
d			100,00			77,59			63,90		68,04	68,04			64,15			60,58

* Perennial species.
a. Number of live individuals present.
b. Number of live individuals present as a percentage of the month's total live plant population = relative abundance.
c. Number of live individuals as a percentage of the largest monthly count for this species during the whole experimental period (6 months)—PMP (Percentage of Maximum Presence).
d. Total number of live individuals on the plot as a percentage of the total number of seedlings that emerged during the whole experimental period (6 months).

Table 5

The size and composition of the population of plot 3 (1 m^2) in the Hester Malan Nature Reserve as determined at monthly intervals from April to September 1974

	April			May			June			July			August			September		
Species	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Cotula barbata	1 558	86,08	100,00	1 419	87,16	91,08	1 332	92,63	85,49	1 293	92,75	82,99	1 269	93,10	81,45	1 254	93,44	80,49
Dischisma spicatum	143	7,90	100,00	109	6,70	76,22	59	4,10	41,25	57	4,09	39,86	51	3,74	35,66	50	3,73	34,96
Phamaceum croceum	67	3,70	100,00	64	3,93	95,52	25	1,74	37,31	24	1,72	35,82	23	1,69	34,33	20	1,49	29,85
Crotalaria micrantha	13	0,72	100,00	8	0,49	61,54	2	0,14	15,38	1	0,07	7,69	1	0,07	7,69	1	0,07	7,69
Polycarena pubescens	13	0,72	100,00	13	0,80	100,00	10	0,70	76,92	10	0,72	76,92	10	0,73	76,92	10	0,75	76,92
Heliophila pectinata	4	0,22	100,00	4	0,24	100,00	3	0,21	75,00	1	0,07	25,00	1	0,07	25,00	0	0,00	0,00
Mesembryanthemum species	4	0,22	100,00	2	0,12	50,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00
Helichrysum obtusum var. obtusum	3	0,17	100,00	3	0,18	100,00	2	0,14	66,67	3	0,22	100,00	3	0,22	100,00	3	0,22	100,00
Ursinia cakilefolia	3	0,17	100,00	3	0,18	100,00	3	0,21	100,00	3	0,22	100,00	3	0,22	100,00	3	0,22	100,00
Mesembryanthemum karrooense	1	0,06	100,00	1	0,06	100,00	1	0,07	100,00	1	0,07	100,00	1	0,07	100,00	1	0,07	100,00
Species 4	1	0,06	100,00	1	0,06	100,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00
Species 5				1	0,06	100,00	1	0,07	100,00	1	0,07	100,00	1	0,07	100,00	0	0,00	0,00
Total	1 810	100,02		1 628	99,98		1 438	100,01		1 394	100,00		1 363	99,98		1 342	99,99	
d			100,00			89,85			79,36			76,93			75,22			74,06

a. Number of live individuals present.

b. Number of live individuals present as a percentage of the month's total live plant population = relative abundance.

c. Number of live individuals present as a percentage of the largest monthly count for this species during the whole experimental period (6 months)—PMP (Percentage of Maximum Presence).

d. Total number of live individuals on the plot as a percentage of the total number of seedlings that emerged during the whole experimental period (6 months).

TABLE 6

The size and composition of the population of plot 4 (1 m^2) in the Hester Malan Nature Reserve as determined at monthly intervals from April to September 1974

	April			May			June			July			August			September		
Species	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Leyssera tenella	1 301	79,62	100,00	1 059	79.03	81,40	961	76,70	73,89	828	73,86	63,64	784	74,38	60,26	753	74,85	57,88
Arctotis fastuosa	194	11,87	100,00	164	12,24	84,54	160	12,77	82,43	160	14,27	82,47	145	13,76	74,74	138	13,72	71,13
Senecio cardaminefolius	29	1,77	100,00	13	0,97	44,83	11	0,88	37,93	9	0,80	31,03	7	0,66	24,14	6	0,60	20,69
Tetragonia microptera	27	1,65	90,00	25	1,87	83,33	30	2,39	100,00	30	2,68	100,00	28	2,66	93,33	26	2,58	86,67
Zaluzianskya benthamiana	19	1,16	100,00	15	1,12	78,95	17	1,36	89,47	15	1,34	78,95	12	1,14	63,16	10	0,99	52,63
Pentzia albida	16	0,98	76,19	15	1,12	71,43	18	1,44	85,71	21	1,87	100,00	21	1,99	100,00	21	2,09	100,00
Galenia filiformis	12	0,73	92,31	12	0,90	92,31	13	1,04	100,00	13	1,16	100,00	13	1,23	100,00	12	1,19	92,31
Erodium cicutarium	10	0,61	100,00	6	0,45	60,00	6	0,48	60,00	5	0,45	50,00	5	0,47	50,00	4	0,40	40,00
Aizoon canariense	7	0,43	63,64	9	0,67	81,82	10	0,80	90,00	11	0,98	100,00	11	1,04	100,00	10	0,99	90,91
Mesembryanthemum karrooense	7	0,43	100,00	5	0,37	71,43	5	0,40	71,43	5	0,45	71,43	5	0,47	71,43	5	0,50	71,43
Pentzia suffruticosa	5	0,31	27,78	12	0,90	66,67	16	1,28	88,89	18	1,61	100,00	18	1,71	100 00	16	1,59	88,89
Schismus barbatus	5	0,31	100,00	3	0,22	60,00	3	0,24	60,00	3	0,27	60,00	1	0,09	20,00	1	0,10	20,00
Ursinia nana subsp. nana	2	0,12	100,00	1	0,07	50,00	1	0,08	50,00	1	0,09	50,00	1	0,09	50,00	1	0,10	50,00
Felicia merxmuelleri				1	0,07	50,00	1	0,08	50,00	1	0,09	50,00	2	0,19	100,00	2	0,20	100,00
Heliophila pectinata							1	0,08	100,00	1	0,09	100,00	1	0,09	100,00	1	0,10	100,00
Total	1 634	99,99		1 340	100,00		1 253	100,02		1 121	100,01		1 054	99,97		1 006	100,00	
d			100,00			80,34			75,12			67,21			63,19			60,31

a. Number of live individuals present.

b. Number of live individuals present as a percentage of the month's total live plant population = relative abundance.

c. Number of live individuals present as a percentage of the largest monthly count for this species during the whole experimental period (6 months)—PMP (Percentage of Maximum Presence).

d. Total number of live individuals on the plot as a percentage of the total number of seedlings that emerged during the whole experimental period.

Table 7

The size and composition of the population of plot 5 (1 m^2) in the Hester Malan Nature Reserve as determined at monthly intervals from April to September 1974

	April			May			June			July			August			September		
Species	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
*Peliostomum virgatum	35	30,43	100,00	27	30,34	77,14	31	42,47	88,57	31	41,89	88,57	28	44,44	80,00	26	44,07	74,29
Osteospermum amplectens	18	15,65	100,00	18	20,22	100,00	18	24,66	100,00	17	22,97	94,44	16	25,40	88,88	16	27,12	88,88
Dimorphotheca sinuata	17	14,78	100,00	12	13,48	70,59	3	4,11	17,82	3	4,05	17,65	2	3,17	11,76	1	1,69	5,88
*Hypertelis salsoloides	17	14,78	100,00	13	14,61	76,47	10	13,70	58,82	9	12,16	52,94	8	12,70	47,06	8	13,56	47,06
Ursinia calenduliflora	5	4,35	100,00	1	1,12	20,00	1	1,37	20,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00
Zaluzianskya benthamiana	5	4,35	100,00	3	3,37	60,00	1	1,37	20,00	1	1,35	20,00	1	1,59	20,00	1	1,69	20,00
Aizoon canariense	4	3,48	100,00	2	2,25	50,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00
Arctotis fastuosa	4	3,48	100,00	4	4,49	100,00	3	4,11	75,00	3	4,05	75,00	1	1,59	25,00	1	1,69	25,00
Osteospermum hyoseroides	4	3,48	100,00	4	4,49	100,00	4	5,48	100,00	4	5,41	100,00	4	6,34	100,00	3	5,08	75,00
*Galenia africana	2	1,74	100,00	2	2,25	100,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00
Lotononis depressa	2	1,74	100,00	2	2,25	100,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00
*Aptosimum indivisum	1	0,87	100,00	1	1,12	100,00	1	1,37	100,00	1	1,35	100,00	1	1,59	100,00	1	1,69	100,00
Species 6	1	0,87	100,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00	0,00
Nemesia azurea							1	1,37	50,00	2	2,70	100,00	1	1,59	50,00	1	1,69	50,00
Species 7										2	2,70	100,00	0	0,00	0,00	0	0,00	0,00
Ursinia nana subsp. nana										1	1,35	100,00	1	1,59	100,00	0	0,00	0,00
Total	115	100,00		89	99,99		73	100,01		74	99,98		63	100,00		59	99,98	
d			100,00			71,77			58,87			59,68			50,81			47,58

* Perennial species.

a. Number of live individuals present.

b. Number of live individuals present as a percentage of the month's total live plant population = relative abundance.

c. Number of live individuals present as a percentage of the largest monthly count for this species during the whole experimental period (6 months)—PMP (Percentage of Maximum Presence).

d. Total number of individuals present on the plot as a percentage of the total number of seedlings that emerged during the whole experimental period (6 months).

As mentioned in the previous paper in this series (Van Rooyen, Theron and Grobbelaar, 1979) in which a general description of the phenology of the vegetation of the area was presented, March was regarded as the beginning of the 1974 growing season for the therophytes, because of the good rains during that month. Growth during the winter months was slow and only after temperatures began to rise in spring, did the growth rate increase. October was regarded as the end of the growing season for therophytes in 1974.

The results of the data collected during the period April to November 1974 are presented in Tables 3 to 7 and Figures 1 to 5.

Germination

During the experimental period by far the most seeds of a particular species and seeds of the largest number of different species germinated after the rains from 10 to 13 March (Tables 3 to 7). As a result no less than 1 558 seedlings of *Cotula barbata* (plot 3), 1 301 seedlings of *Leyssera tenella* (plot 4) and 859 seedlings of *Micropterum papulosum* (plot 1) were counted in the plots in April. Between the April and May counts, only a few seeds of a small number of species germinated, whereas a fairly large number of seedlings emerged between the June and July counts. Among the seedlings which emerged in June, presumably as a result of the 28,7 mm of rain which fell early in June, those of *Heliophila pectinata* were especially abundant. During the next two months (July and August) only a few seeds of a small number of species germinated.

For all plots it was found that the density of the total number of seedlings per plot was the highest during April, when the counts ranged from 115 seedlings per m^2 (plot 5) to 1 810 seedlings per m^2 (plot 3). The highest density that was recorded for a single species was 1 558 seedlings per m^2 (plot 3) for *Cotula barbata* during the April count. Compared with the results from other deserts or semi-deserts in California, these densities are not particularly high. Went and Westergaard (1949) recorded up to 5 000 seedlings per m^2 in the Death Valley National Park, while Tevis (1958b) found a total of up to 1 112 seedlings per m^2 in the Sonoran Desert. In Mendocino County, Heady (1956) recorded 54 250 plants per m^2 (35 per square inch) whilst Biswell and Graham (1956) found 224 696 seedlings per m^2 (20 875 per square foot) in dense stands of *Festuca megalura* in Madera County.

Survival

The PMP-values* (Tables 3 to 7) of the most conspicuous species in each plot for the period April to September 1974 are diagramatically presented in Figures 1 to 5. For most species there was a decrease in the number of individuals per plot from one count to the next. Because of the increase in volume of the surviving plants this reduction in numbers was not so noticeable in the field. The monthly PMP-values of a species indicate the percentage of individuals surviving. In the case of the therophytes the September PMP-values represent the percentage of each species which completed its life cycle successfully.

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*Percentage of Maximum Presence—number of live individuals present as a percentage of the largest monthly live count for this species during the whole experimental period.

Results show that the percentage of the whole population that survived from April to September varied from 47,58 % (plot 5) to 74,06 % (plot 3) between plots. For the different species within a plot, the number of seedlings which developed into mature plants varied from 0,00 % to 100,00 % of the total that emerged.

Survival of species on a study site, *i.e.* at least one individual of the species reached maturity on the study site, ranged from 62,5 % (plot 5) to 100,00 % (plot 4) between plots. If, however, the results of all plots are considered together, *i.e.* at least one individual of the species reached maturity at any of the study sites, the percentage survival of species was 85,3 %.

The PMP-values for a given species were not always constant for the different sites. These differences in survival for the same species can possibly be related to differences in the micro-environment of the sites. For instance, the percentage survival of *Tetragonia microptera* was 21,82 % at plot 1; 44,53 % at plot 2 and 86,67 % at plot 4. On the other hand, *Dischisma spicatum* showed a rather constant percentage survival for plots 1 and 3, the values being 34,62 % and 34,96 % respectively.

The variable response of the species to the environment is reflected in the differences in percentage relative abundance in successive months at one study site (Tables 3 to 7). Provided the total number of individuals at one site does not increase in successive months due to the emergence of new seedlings, one can deduce that a species is well adapted to the environment if the number of live plants as a percentage of all the live plants in the plot, increases from one month to the next. For instance, the relative abundance of *Osteospermum hyoseroides* and *Erodium cicutarium* consistently increased during the whole experimental period in plot 1 and these species can therefore possibly be regarded as being better adapted to the environment than many of the other species also occurring in the plot. Conversely, if, in the absence of further seed germination within the plot, the relative abundance of a species decreases in time, this could signify that relative to the other species in the plot, this species is not so well adapted to the prevailing environmental conditions. From the present results it would therefore appear that *Dischisma spicatum*, *Pharnaceum croceum* and *Crotalaria micrantha* were not so well adapted to the environment as the other species in plot 3. In the case of *Dimorphotheca sinuata* in plot 5, the decrease in relative abundance during the six month period, appeared to be due to selective grazing by animals.

Of the total of 5 056 seedlings encountered in the five plots during the period from April to September, 63,59 % survived. This represents a somewhat better survival value than has been reported for other arid regions. Despite the fact that

Juhren, Went and Phillips (1956) conclude that "most seedlings survive", their results for the Joshua Tree National Monument in California show a range of 9–71 % survival on different sites and of the total original seedling population only 46 % survived. The results of Tevis (1958b) for the Coachella Valley, Sonoran Desert in California show survival values from 0–73 % for 12 different species and of the total original seedling population 49,78 % reached maturity. Beatley (1967) working in the northern Mojave Desert in southern Nevada, reported that the percentage seedlings that reached maturity in two successive years was 38 % and 60 % respectively. The growing seasons in the two cases were 7 to 8 months and 6 to 10 weeks respectively. These two growing seasons represent the extremes in length which appear possible for winter annuals of that region (Beatley, 1967)

Mortality

A decrease in time of the PMP-value (Tables 3 to 7 and Figures 1 to 5) for a given species represents the approximate mortality of that species during the period. The true mortality can, however, be higher than the approximate value if new seedlings emerge while others perish in the same month. As this rarely happened to a significant extent during one month, the approximate value for the monthly mortality of a species generally can be regarded as the true mortality for the month. According to these values the largest number of individuals died in the plots during April and May.

The mortality rate, however, should be expressed as the number of individuals perishing during one month as a percentage of the number of individuals present in the beginning of the month. The mortality rate of the different species does not show a constant pattern, neither does it seem possible to correlate the mortality rate with any environmental factors. All stages in the life cycle of a plant are not necessarily equally sensitive to unfavourable environmental factors and this probably explains the lack of an obvious mortality pattern.

Tevis (1958b) reported that the only significant cause of mortality for any species was moisture-stress, whereas Beatley (1967) states that the fate of any given individual is apparently related to its location relative to microvariations in moisture in the upper 80 to 200 mm of soil and to the effectiveness with which its root system penetrates the soil volume in advance of others.

As a possible explanation for the differences in species composition of therophyte populations from year to year, it has been suggested that the temperatures prevailing at the time of the infrequent rainfall, determine which species will germinate (Went, 1948, 1949; Went and Westergaard, 1949; Juhren, Went and Phillips, 1956; Tevis, 1958a, 1958b). This statement is based on the fact that each species has its own and often very narrow requirements for germination. As a result of favourable rainfall-temperature combinations one species may dominate

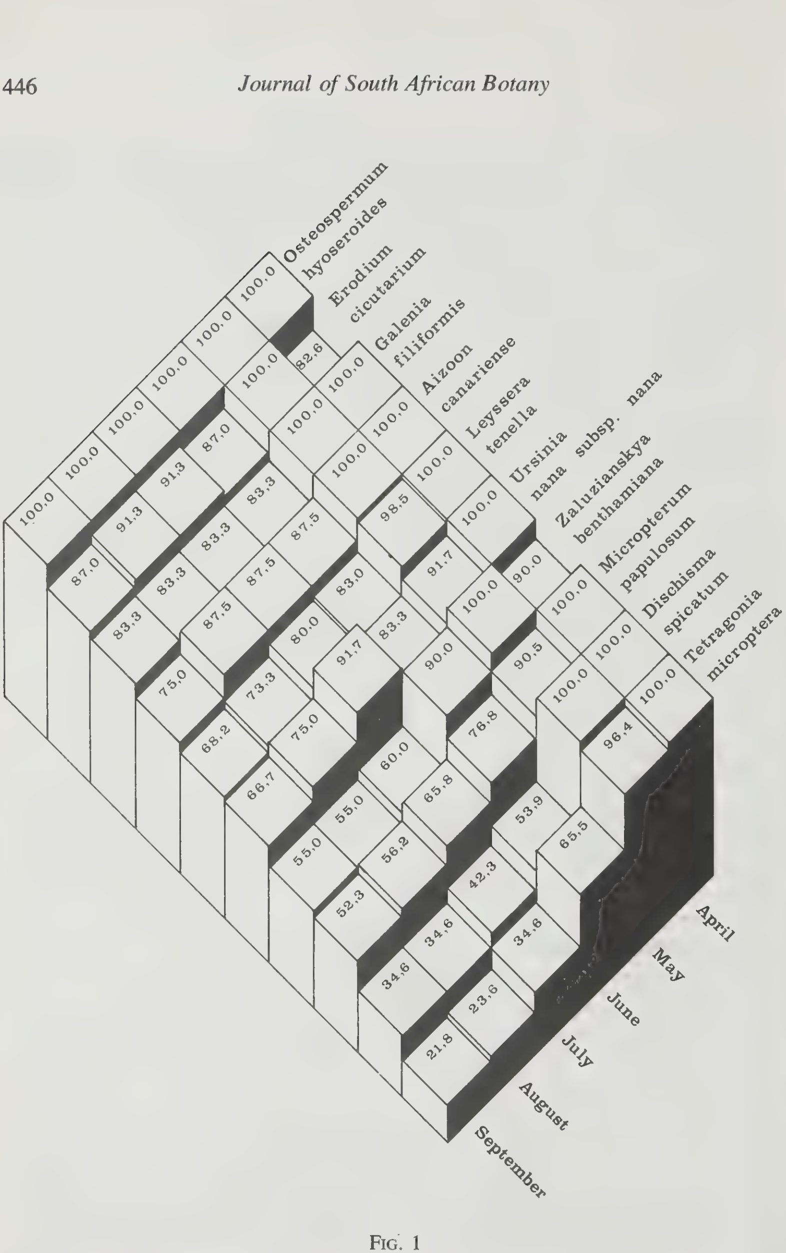

FIG. 1
The PMP-values (Percentage of Maximum Presence) of the most conspicuous species in plot 1 in the Hester Malan Nature Reserve from April to September 1974.

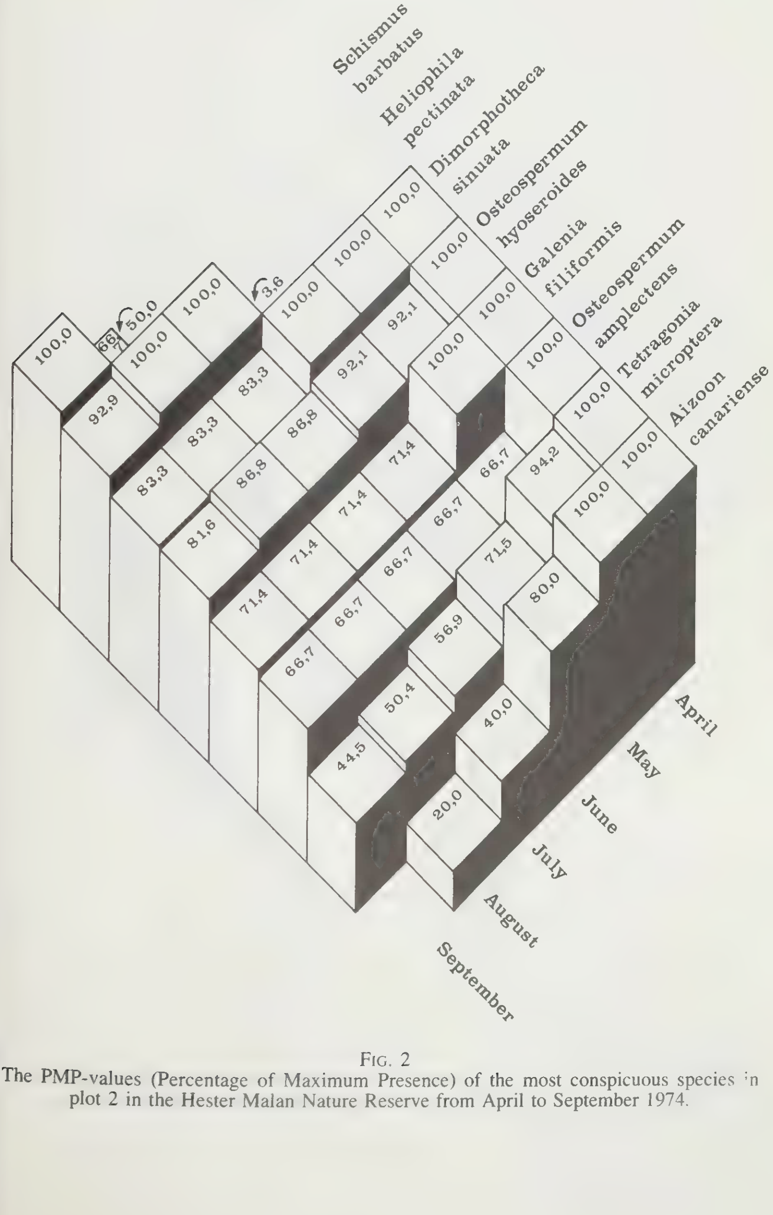

FIG. 2
The PMP-values (Percentage of Maximum Presence) of the most conspicuous species in plot 2 in the Hester Malan Nature Reserve from April to September 1974.

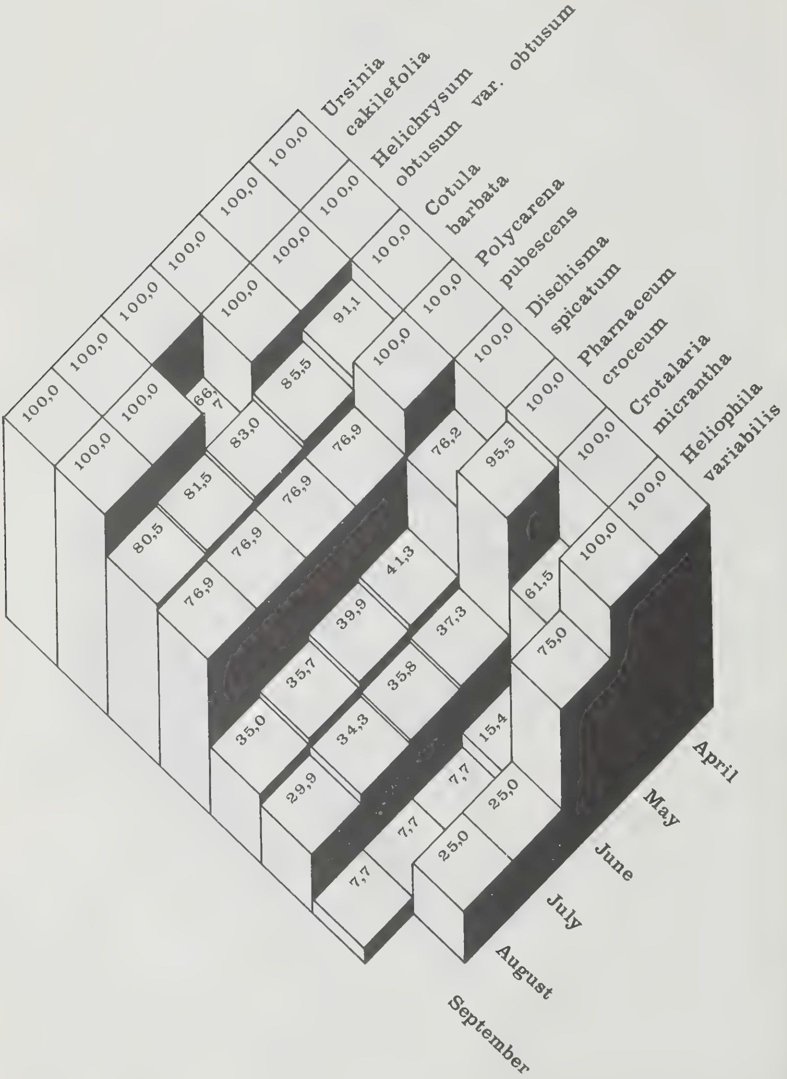

FIG. 3
The PMP-values (Percentage of Maximum Presence) of the most conspicuous species in plot 3 in the Hester Malan Nature Reserve from April to September 1974.

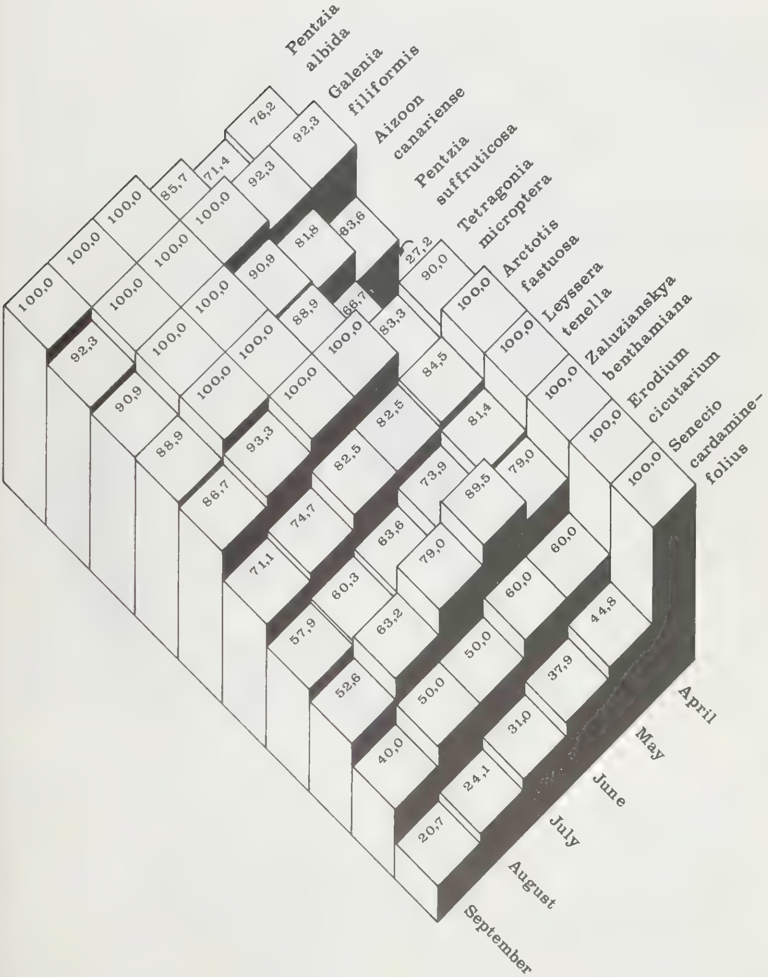

FIG. 4
The PMP-values (Percentage of Maximum Presence) of the most conspicuous species in plot 4 in the Hester Malan Nature Reserve from April to September 1974.

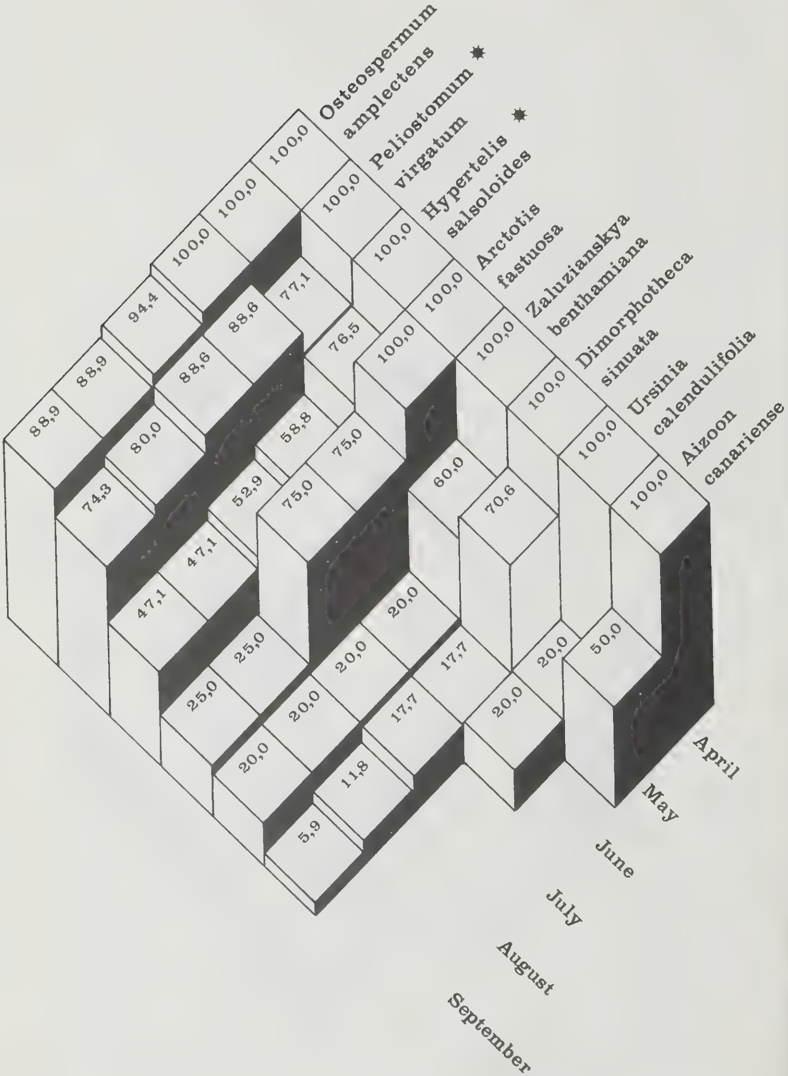

FIG. 5
The PMP-values (Percentage of Maximum Presence) of the most conspicuous species in plot 5 in the Hester Malan Nature Reserve from April to September 1974. Perennial species marked with an asterisk.

the landscape in one year; while in the next year, they may hardly be noticeable at all and quite a different species may appear to be dominant.

SUMMARY

In the beginning of April 1974 five 1 m^2 plots were laid out and all seedlings in the plots were mapped and counted. The plots were visited at monthly intervals and all new seedlings were added and the death of others noted. From these results the following values were calculated for each species:

monthly percentage of maximum population (PMP-value);
monthly relative abundance; and
monthly mortality rate (not included in Tables 3 to 7).

The largest number of seeds germinated in March and densities from 115 to 1 810 seedlings per square metre were reported on the plots in the beginning of April. A relatively small number of seeds germinated later during the season.

Of the total of 5 056 seedlings found in the plots 3 215 (63,59 %) reached maturity. The percentage survival of individuals at one site ranged from 47,58 % to 74,06 % between plots and from 0,00 % to 100,00 % between species. If the results of all the plots are considered together the percentage survival of species was 85,3 %.

An increase or a decrease in the relative abundance of a species indicates the adaptability of a species to the prevailing environmental conditions as compared with the other species also occurring in the same plot.

The largest number of individuals died during April and May but no clear correlations could be demonstrated between the mortality rate and abiotic environmental conditions.

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REFERENCES

BEATLEY, JANICE C., 1967. Survival of annuals in the northern Mojave Desert. *Ecology* **48:** 745–750.

BISWELL, H. H. and GRAHAM, C. A., 1956. Plant counts and seed production on California annual-type ranges. *J. Range Mgmt.* **9:** 116–118.

BYKOV, B. A., 1974. Fluctuations in the desert and semi-desert vegetation of the Turanian Plain. In: Knapp, R. (ed.), *Handbook of vegetation science*. 8. *Vegetation dynamics*. pp. 243–251. The Hague: Junk.

HEADY, H. F., 1958. Vegetational changes in the Californian annual type. *Ecology* **39:** 402–416.

JUHREN, MARCELLA, WENT, F. W. and PHILLIPS, E., 1956. Ecology of desert plants. 4. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. *Ecology* **37:** 318–330.

Loxton, R. F., 1966. *A simplified soil-survey procedure for farm planning*. Pretoria: Government Printer.

Rösch, Margaretha W., 1977. *Enkele plantekologiese aspekte van die Hester Malan-natuurreservaat*. M.Sc. thesis. Pretoria: University of Pretoria.

Talbot, M. W., Biswell, H. H. and Hormay, A. L. 1939. Fluctuations in the annual vegetation of California. *Ecology* **20:** 394–402.

Tevis, L. Jr., 1958a. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology* **39:** 681–688.

Tevis, L. Jr., 1958b. A population of desert ephemerals germinated by less than one inch of rain. *Ecology* **39:** 688–695.

Van Rooyen, Margaretha W., Theron, G. K. and Grobbelaar, N., 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld: 1. General observations. *Jl S. Afr. Bot.* **45:** 279–293.

Went, F. W., 1948. Ecology of desert plants. 1. Observations on germination in the Joshua Tree National Monument California. *Ecology* **29:** 242–253.

Went, F. W., 1949. Ecology of desert plants. 2. Effect of rain and temperature on germination and growth. *Ecology* **30:** 1–13.

Went, F. W., 1955. The ecology of desert plants. *Scient. Am.* **193:** 68.

Went, F. W. and Westergaard, M., 1949. Ecology of desert plants. 3. Developments of plants in the Death Valley National Monument, California. *Ecology* **30:** 26–38.